30
6
10

ESSAYS

ON THE

CONARIO-HYPOPHYSIAL TRACT

AND ON THE

ASPECTS OF THE BODY

IN

VERTEBRATE AND INVERTEBRATE ANIMALS.

BY

RICHARD OWEN, C.B., F.R.S., F.L.S., ETC.

c

LONDON:

TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

1883.

ALERE FLAMMAM.

PRINTED BY TAYLOR AND FRANCIS,

RED LION COURT, FLEET STREET.

MOTIVE.

The prescient glimpse of the principle "l'Unité de Composition Organique" in the Animal Kingdom, which guided the labours of Geoffroy St.-Hilaire, and was propounded in his first contribution* to a 'Philosophie anatomique,' called forth the comments of his ablest contemporaries. Of these the article by Flourens† discusses the subject in relation to the Vertebrate type. Geoffroy's subsequent volume illustrative of his ruling idea by the phenomena of "Monstruosities" was the subject of a similar favourable analysis by Frédéric Cuvier‡.

To the difficulties which the Invertebrates seemed to Dugès to oppose to an acceptance of Geoffroy's generalization he replied§, by reference to "fig. 2 de la septième planche :—Là se trouve effectivement représenté un homard couché sur le dos et montrant distinctivement ses viscères dans la position où le sont les viscères des mammifères placés sur le ventre"||.

Hereupon Baron Cuvier intervened, with the object set forth and illustrated in his notable paper in the 'Annales des Sciences Naturelles,' referred to in the first of the following essays.

This phase of the discussion, which I was favoured, in 1831, to hear in the Hall of the Institute allotted to the Académie des Sciences, has seldom since been absent from my thoughts in connexion with any observations and researches which seemed to throw light upon it. The exposition of the nature of the structures which Cuvier deemed fatal to Geoffroy's illustration of his principle is the chief subject of the two following essays.

* "Des organes respiratoires, sous la rapport de la détermination et de l'identité de leurs pièces osseuses."

† 'Analyse de la Philosophie anatomique,' 8vo, 1819.

‡ In 'La Revue encyclopédique,' tom. xvii. Février 1823.

§ In the Part "Sur la Vertèbre," 1822.

|| "Lettre sur quelques points du Mémoire ayant pour titre : De la Conformité organique dans l'Echelle animale," in 'Gazette Médicale de Paris,' No. 44, 1831, p. 4.

PINEAL AND PITUITARY BODIES.

CHAPTER I.

HOMOLOGY OF THE CONARIO-HYPOPHYSIAL TRACT.

THE structure and local relations of the pituitary and pineal bodies, in Man, have received such close attention in anthropotomical works as to dispense with repetition. But, before entering upon the special aim of the present Chapter, I feel bound to refer to the latest contribution to the subject, that, viz., by Dr. Joseph Sapolini*, who has devoted a special treatise to one portion of the "tract" in question.

He more especially points out the continuation of the "third ventricle" of the brain by its tubular extension downward, called the "infundibulum," with the substance of the "pituitary gland," the texture, the blood-vessels, nerves, and osseous environment of which body in Man are minutely described and amply illustrated. The chief aim of these researches, however, is a teleological one; and the author arrives at the conclusion that the function of the so-called "gland"† is secretory, and that it relates to the supply of the intraventricular fluids of the brain.

Referring to the course from the third ventricle, by the infundibulum, to a cavity or reservoir in the hind lobe of the

* 'L'aire de la Selle Turcique,' 8vo, 1880.

† The term "pituitary" was originally applied thereto on the notion that it secreted the mucosity lubricating the nasal passages.

pituitary*, he concludes that the fluid secreted by the fore lobe accumulates in the "reservoir," and that, by vermicular movements of the gland, governed by the filaments of the sixth cerebral nerve, which he traces thereto, the fluid it secretes ascends, and passes by the tubular or infundibular continuation of the gland into the third, and thence into the fourth and other continuous vacuities or ventricles of the brain and myelon†.

"May we not then," he asks, "compare the pituitary gland to the liver, and its cavity to the gall-bladder?" ‡.

To this appeal, Dr. Sapolini, whose treatise issues from a Brussels press, may reasonably look for an affirmative response from the accomplished Professor of Liége. M. Ed. Van

* "C'était mon aniline qui, depuis le troisième ventricule, était descendue à travers l'infundibulum et le canal de la tige pituitaire, jusqu'à la cavité de la glande. Ceci établit qu'il y a une parfaite communication entre la partie centrale du lobule du corps pituitaire et le troisième ventricule cérébral."—*Op. cit.* p. 63.

† "A l'état physiologique il existe toujours dans les ventricules cérébraux un liquide incolore, inodore, insipide. Ce liquide non seulement peut, mais par moments doit, se mettre en mouvement; alors il dépasse dans sa course l'aquéduc de Sylvius, et suivant l'inclinaison du quatrième ventricule, il descend le long du canal rhachidien en passant par le trou du calamus scriptorius. Ce liquide, à l'état normal, augmente par instants dans les ventricules, et ce sera dans le troisième que se déversera le trop plein des autres."—*Op. cit.* p. 63.

‡ "Le lobe antérieure de la glande sécréterait donc le liquide qui se rendrait et s'accumulerait dans le réservoir du lobe postérieur; il passerait ensuite par la valvule de la tige pituitaire qui peut et doit s'ouvrir; de là il montrait dans la tige elle-même qui est douée des mouvements vermiculaires, car elle est animée par des filets nerveux émanant du nerf de la sixième paire. Le corps pituitaire ne serait-il donc pas semblable, pour employer une comparaison hyperbolique, au foie qui sécrète la bile, et sa cavité à la vésicule biliaire qui est le réservoir de celle-ci?"—*Op. cit.* p. 64.

Beneden*, referring to the body in Tunicaries (Savigny's "tubercle," Hancock's and Ussow's "olfactory organ"), which is homologized by M. Julin† with the "pituitary gland" of Vertebrates, compares it to the kidney, and holds that by a communication with the "peribranchial cavity" of the Ascidian it discharges its urinary excretion therein. Lacaze-Duthiers describes a similar, or the same, "glandular organ" in juxtaposition with the ciliated sac in the "Simple Ascidians"‡. Balfour deems it "possible that this organ, as well as the ciliated sack, may be related to the pituitary body"§. Of the function of that body in the Vertebrate series the latter embryologist entertains a view "as possible," viz., that "the pituitary body is a glandular structure, which originally opened into the mouth in the lower *Chordata*" (syn. *Vertebrata*), "but which has, in all existing forms, ceased to be functional"‖. The alternative view is as follows:—"The true nature of the pituitary body has not yet been made out. It is clearly a rudimentary organ in existing craniate Vertebrates, and its development indicates that, when functional, it was probably a sense-organ opening into the mouth"¶.

The impression left by results of observations, presently to be submitted, leads me to define the pituitary body rather as a "residuary" than a "rudimentary" organ. At least I

* Archives de Biologie, 8vo, 1881, tom. ii. fascicule ii. p. 230.

† *Ibid.* fascicule i. p. 59 *et seq.* (I may remark that, regarding the cylindroid shape as well as position of the neural centre in some Ascidians, I have viewed it as the homologue of the same part in *Amphioxus*, and the co-extensive body beneath as indicative of the notochord.)

‡ "Les Ascidies simples des Côtes de France," Archives de Biologie expérimentale et générale, vol. iii. 1874, p. 329.

§ Treatise on Comparative Embryology, 8vo, 1881, vol. ii. p. 360.

‖ *Ib. ib.* p. 360. ¶ *Ib. ib.* p. 359.

have failed to detect in any of the modifications of the part, in Vertebrates, homologous with the pituitary body in Man, evidence of a nervous or glandular part, superadded, for example, to the structure of the lining or mucous membrane of an alimentary canal and to the neural filament endowing such secreting surface with sensibility. Into the materials of the subsequent obliteration, with plethoric consolidation, of the transitory tube neither secerning sacs nor nerve-cells enter.

Swedenborg, who had extended his studies of the nervous system from Man to Insects, held that "the pineal gland, the infundibulum, and the pituitary gland elaborated the white or lymphatic blood of the brain," and that the pineal body exercised the following more special office :—"The aqueduct under the corpora quadrigemina is a receptacle of the lymph of the third ventricle, which, through a foramen, over which the pineal gland exercises control, pours its liquid stream"*. Henlé, like Swedenborg, views the "pineal" as a lymphatic gland. Meynert regards it as "a ganglion originating the tegmentum-cells which are of two sizes." Majendie concluded its function to be mechanical; that "the pineal acted as a kind of plug, obstructing the communication between the third and fourth ventricles." Balfour states that "no satisfactory suggestions have yet been offered as to the nature of the pineal gland;" but, referring to its position external to the skull in Amphibia, he says that it there "forms a mass originally described by Stieda as the 'cerebral gland'"†.

The researches of which I proceed to communicate results

* 'The Brain considered Anatomically, Physiologically, and Philosophically.' By Emanuel Swedenborg. 4 vols., 8vo, 1882. Edited by R. L. Tafel, A.M., Ph.D.

† *Op. cit.* vol. ii. pp. 257, 258.

have been conducted with other than teleological aims: they have led me to trace both the pineal and pituitary bodies, their appendages and connections, or what I have termed the "conario-hypophysial tract," from Man downward, until, in *Amphioxus*, where the cerebral expansion of the myelencephalon is too feebly indicated, the homologue of any part of the tract in question has baffled my quest—unless the pore or ciliated canal leading thereto may be in such relation.

In the Mammalian series I have to observe that, in the lower and smaller members, as the brain loses in relative size and complexity, the pineal or conarial and pituitary or hypophysial bodies and connections show a relatively larger size, with a less parenchymatous and a less interrupted tubular structure than in the human brain. In the lower, if not lowest, forms of the feathered class I have noted a character of the basisphenoid which seemed to me to bear upon the present topic: it is a median longitudinal groove leading to a foramen opening into the seat of the pituitary body*.

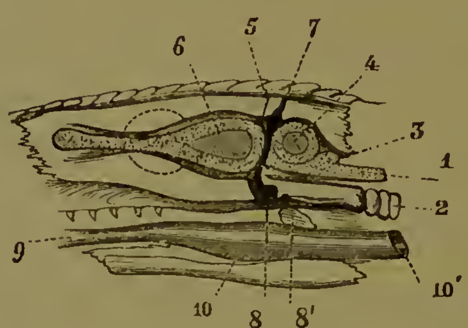
But leaving here the class of Birds in the present summary, the proportions of the conario-hypophysial tract to the cerebral hemispheres in Reptiles become greater, and a vascular chord is continued upward from the hollow "pineal" part of the tract, beyond the cleft between the pros- and mesencephalon, to a contiguous opening in the bony cranial roof in a proportion of the class, which proportion is greater in the extinct members†. This "pineal" production perforates, as a rule, the parietal bone, but in some species the suture between

* See 'Memoirs on the Wingless Birds of New Zealand,' 4to, 1878: *Dinornis elephantopus*, pl. lxxvi. fig. 4, 5; *D. crassus*, pl. lxxvii. fig. 3, 5; *D. ingens*, pl. lxxxii. fig. 3, 5; *D. gravis*, pl. lxxxi. fig. 4,—in which the foramen, not eustachian, is unusually and significantly large.

† See 'Monograph on *Ichthyopterygia*,' Palæontographical Society's volume for 1881, 4to, p. 94, pl. xxiii. fig. 1, *f*; also "Descriptive and

that bone and the frontal, rarely the frontal bone itself, and then near the suture, always opposite the interval between the fore and mid brains. Beyond this hole, commonly called "foramen parietale," but which may preferably be termed "foramen pineale," the upward continuation of the conario-hypophysial tract or tube (fig. 1, 7, 8) is closed by the scalp or supracranial integument.

Fig. 1.



Section of cranium and brain of young *Iguana*, showing foramen parietale &c.—1. Neural axis. 2. Vertebral column. 3. Cerebellum. 4. Optic lobe. 5. Thalamencephalon. 6. Cerebrum. 7. Pineal body. 8. Pituitary body—conario-hypophysial tract (including "infundibulum" and "third ventricle"); 8' indicates the "protopharynx" of the embryo. 9. Mouth. 10. Gullet.

To the embryologist the so-called "pineal gland" first manifests itself as a hollow pyramidal or papillary extension of the roof of the large mid-cerebral vesicle, or "thalamencephalon" (fig. 4, 5). In the cold-blooded Vertebrates it inclines forward; in Mammals and to some extent in Birds it is directed backward. In all it seems in quest of an open

---

Illustrated Catalogue of the Fossil Reptilia of South Africa in the British Museum," showing the parietal or "pineal" foramen in the genera *Galesaurus*, *Petrophryne*, *Dicynodon*, *Ptychognathus*, *Oudenodon*, *Kistecephalus*, and *Procolophon*: in some of these genera the hole is unusually large.

or oral outlet, but is checked by the external skin in lower forms, and by the cranial roof of the brain in the higher ones. Where its course is not so arrested, the peripheral and expanded part becomes consolidated; and such mass has been described, like the similarly modified opposite or internal portion of the abortive gullet, as a gland.

In the class of Fishes the relative magnitude and tubular character of this transcerebral tract is still more marked, examples of which I have elsewhere described and figured*.

According to Prof. Ehlers, "Die Epiphyse am Gehirn der Plagiostomen," the representative of the pineal body, appears as an elongate membranous tube opening at one, the central, end into the mid brain, and expanding at the peripheral end, where the canal is arrested either by the cranial cartilage, in a cavity of which it is lodged, or by the epicranial skin after perforation of the cranium.

The relative dimensions of this abortive pharynx remain greatest in the still lower fishes. In the Ammocetes the walls of the peripheral part of the "pineal" canal are plicate: in the Lampreys the canal, arrested after traversing the mid brain, retains a sac-like expansion which extends both backward and forward beneath the skin of the head.

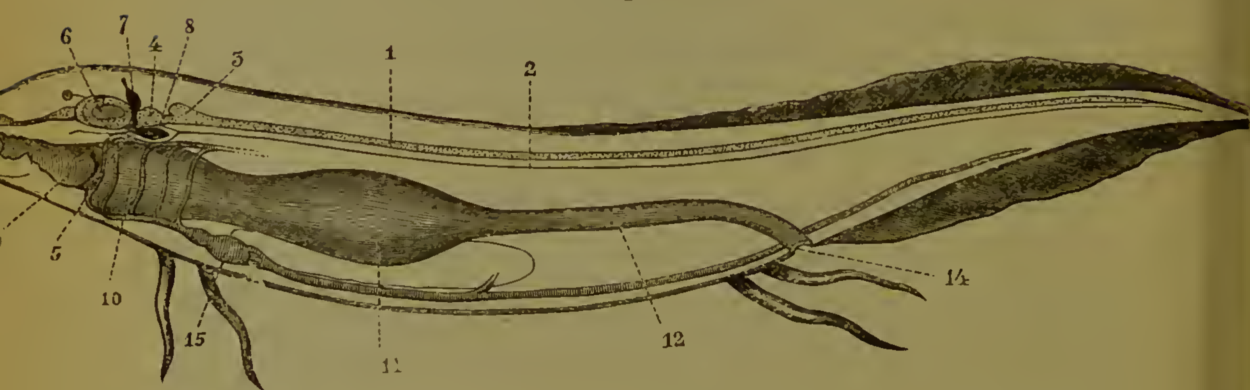
The further change in this abortive pharynx is the closure of its lumen, and the conversion of the tube into a cord, which retains, after traversing the epicranium, its larger proportions, and forms the mass which, in Amphibia and Reptilia, is called "cerebral gland" (*ante*, p. 4); but this term is as applicable to the pituitary as to the pineal body.

"The true vasculo-membranous infundibuliform downward

* 'Anatomy of Vertebrates,' 8vo, vol. i. 1866, p. 277. "The third ventricle in Osseous Fishes is prolonged downward into the pedicle of the hypophysis or 'pituitary gland,' fig. 185, *p*, and upward into that of the conarium or 'pineal gland,' fig. 175, *w*."

prolongation of the third ventricle exists in all Osseous Fishes. The 'infundibulum' is commonly short and thick, so that the hypophysis is almost sessile, as in the Cod; but in the *Lophius* the infundibulum is longer than the entire brain, and the hypophysis lies at the fore part of the cranial cavity far in advance of the cerebral lobes (but in vertical parallel with the palate). In the Cod the hypophysis, fig. 185, *p*, is a subspherical mass, with an irregular surface almost half the size of the human 'pituitary gland,' and illustrating the vast proportional size of this constant appendage to the brain of Fishes"*.

Fig. 2.



Protopterus.—1. Neural axis. 2. Notochord. 3. Cerebellum. 4. Optic lobe. 5. Foremost branchial arch. 6. Cerebrum. 7. Pineal body. 8. Pituitary body (together, the conario-hypophysial tract). 9. Oral cavity. 10. Branchial cavity. 11. Stomach. 12. Intestine. 14. Vent. 15. Heart and chief blood-vessels.

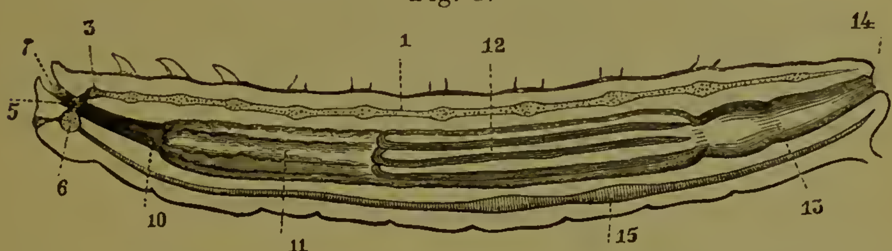
In the Skate (*Raia batis*) the extension of the pineal part of the tract in question reaches beyond the cartilaginous roof of the brain-case; in the spiny Dogfish (*Acanthias*) its progress is there arrested; but the cavity in which it is lodged testifies to its destination, and here it retains, as a dilated part, more of its primal character. In all the Elasmobranchs the pineal part of the arrested gullet is an elongate tube, dilated at its

* Anat. Vert. i. p. 280.

free or peripheral end and maintaining its communication with the "ventricle," from the floor of which the "infundibulum" extends to join the pituitary body. In *Protopterus* (fig. 2), the first-found member of which was referred to the Amphibia under the name "*Lepidosiren*," and belongs to the same collective "Branchiate group" *, the width and length of the "infundibulum" continued from the flattened discoid body, 8, cut off from the bucco-branchial cavity, 9, 10, by a thin lamelliform extension of the basis cranii, is continued by a proportionally wide "third ventricle" into the base of a conical "conarium," 7, as large as the cerebellum itself, from the apex of which conarium a vascular membranous tubule is continued upward and forward through a gristly part of the cranium to the scalp †.

The homology thus suggested of the conario-hypophysial tract in Vertebrates with a vascular canal traversing a cor-

Fig. 3.



Larva of Sphinx.—1. Neural axis. 3. Hind brain. 5. Connecting tracts or "crura," of 6, Fore brain. 7. Neural mouth, or neurostome. 7–10. Pharynx and gullet. 11. Stomach. 12. Hepatic intestine. 13. Rectum. 14. Vent. 15. Heart and chief blood-vessels.

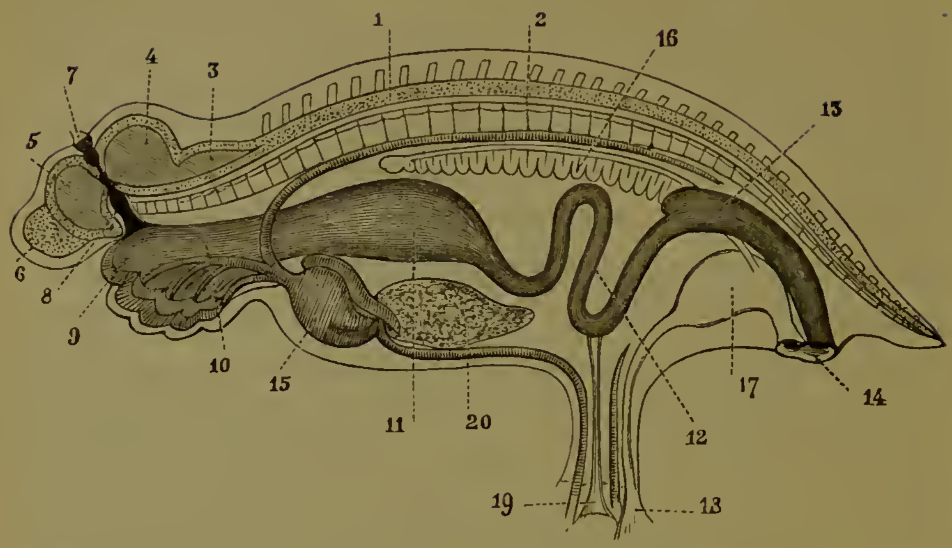
responding part of the brain in Invertebrates (fig. 3, 7, 10), called for further evidence; and such has been amply yielded by Embryology.

In the Vertebrate embryo (fig. 4) the myelencephalon, 1–6, first appears as a longitudinal channel of the epiblast, opening "neurad;" and soon, by upward or neural extension and

* Anat. of Vert. vol. i. pp. 6, 7.

† *Tom. cit.* p. 282, fig. 186.

Fig. 4.



Mammalian embryo.—1. Neural axis. 2. Vertebral axis. 3. Cerebellar vesicle and medulla oblongata = epencephalon. 4. Optic vesicle = mesencephalon. 5. Thalamencephalon, or vesicle of third ventricle. 6. Cerebral vesicle = prosencephalon. 7. Pineal portion, 8. Pituitary or infundibular portion, of the conario-hypophysial tract. 9–10. Bucco-branchial cavity. 11. Stomach. 12. Small intestine. 13. Large intestine. 14. Vent. 15. Heart and chief blood-vessels. 16. Primordial kidney. 17. Urinary bladder. 18. Pedicle of allantois. 19. Pedicle of umbilical vesicle. 20. Liver.

convergence of its side-walls, it is converted by their confluence into a tube.

Passing over the histological steps in the formation of the grey and white matters—" columnar " being converted into " multipolar " cells—and the reduction thereby of the canal to the minute central one of the adult myelon, what here concerns my argument is the progressive forward extension of the cord, with corresponding expansions into the beginnings of the " hind brain," or epencephalon (fig. 4, 3), of the mid brain or mesencephalon (*ib.* 4), and of a large vesicle, " thalamencephalon " (*ib.* 5), dividing the latter from the fore brain, or " prosencephalon " (*ib.* 6). All these expansions, as shown

in the diagram (fig. 4), are hollow ; but the relative size of the cavity, of the so-called "third ventricle" (5), is now the largest of the embryonal cerebral vesicles ; and this disproportion moreover coincides with an incomplete phase of the Vertebrate alimentary canal ; and, what is more to the present contention, the huge homologue of the "third ventricle" extends into two productions of its wall—one downward (8) to a canal, "infundibulum," now communicating with the part in contact with the anterior end of the digestive cavity (9); the other upward (7) to the tubular or sacciform condition of the later pineal body*.

I next pass to the phenomena of the development of the digestive cavity. What subsequently becomes an alimentary canal, begins like the myelon, as a groove, parallel therewith, but opening in the opposite direction, or "hæmad," and there communicating with the vitellicle. It is developed most conspicuously or in greatest proportion from the hypoblast. As the alimentary rudiment extends beyond the yolk-sac, forward and backward, it becomes tubular: an outlet first appears at the end, which led its discoverer to term it "anus," now known as the "blastopore;" but, as the canal elongates, it becomes closed at both ends. It absorbs, or receives, nutriment from the yolk-bag, which recedes as it

* In his exemplary monograph 'On the Development of Elasmobranch Fishes' (8vo, 1878) Mr. Balfour writes :—"During stage L the infundibulum becomes much produced, and forms a wide sack in contact with the pituitary body, and its cavity communicates with that of the third ventricle by an elongated slit-like aperture" (p. 176). . . . "During the same stage the pineal gland grows into a sack-like body" (p. 177). . . . At a later stage (P)—"The pineal sack has also become greatly elongated, and its somewhat dilated extremity is situated between the cerebral rudiment and the external skin. It opens into the hind end of the third ventricle, and its posterior wall is continuous with the front wall of the mid-brain" (p. 177).

diminishes and becomes excluded from the abdomen by completion of the walls of that cavity, save where the primitive yolk-canal, fig. 4, 10, passes on to the shrunk vitellicle, now shut out as an appendage, ultimately to be absorbed or cast off at birth. Here, therefore, besides the transitory vent, we have a primordial "mouth" and "gullet," or parts holding functionally, for a brief period, those relations to the digestive sac. The persistent indication of such course of the embryonal food is called "umbilicus:" it points to one inlet of food which has made way for another; and that other will make way for a third. As well devote pains and speculation to the "function" of the navel as to analogous remnants of a later communication with the alimentary canal, doomed likewise to obliteration with concomitant solidification of parts.

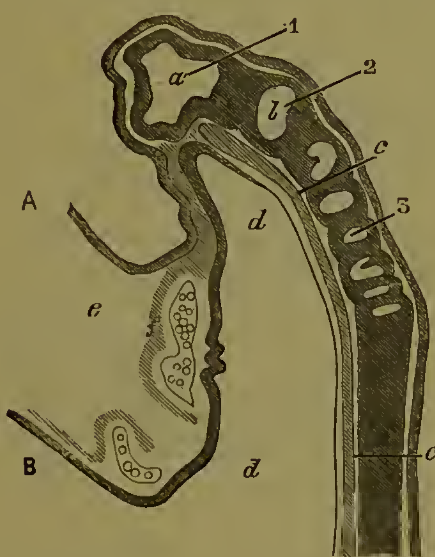
In low radiate forms of life, *Medusa* e. g., the vitelline entry, or "protostome," is permanent; a "deutostome" may, in like manner, appear as another step in the rising scale which is not parted with.

But to return to our Vertebrate grade. The alimentary tube, parallel with the myelonal one, communicates or anastomoses therewith; a common canal thus results, but of which the hæmal portion will be modified to give sustenance to the body, the neural portion to the mind. In the course of differentiation the caudal intercommunion is abolished, the "blastopore" being partially annexed by the neural canal. The anterior end of the alimentary tube (fig. 4, 11), extending forward, comes into close contact and continuity with the canal, which may be described as commencing below at the part which becomes the "pituitary" and its continuation the "infundibulum;" thence continuing upward (neurad) by the third ventricle to the base or origin of the pineal production of the thalamencephalon, which production, perforating, as in the embryo Iguana, the soft lamellar basis of

the cranial roof-bones, is only arrested in its aim to form a mouth, or "deutostome," at the vertex, by failing to overcome the resistance of the superincumbent epithelial layer—such resistance being encouraged by the processes now on foot to establish an external communication, elsewhere, with the fore part of the alimentary canal.

Embryological researches, subsequent to those given in the 'Memoir,' communicated, September 5th, 1881, to the

Fig. 5.



British Association at the York meeting, have concurred in demonstrating the extension of the primary alimentary canal "cephalad" and "neurad," prior to the hæmal opening into the wide branchial space or sac. I take the two illustrations, figs. 5 and 6, from the valuable paper "Du Développement des Ventes et Arcs Branchiaux chez l'Embryon," by Professor Cadiat*.

The extension of the fore part of the alimentary canal in

* 'Journal d'Anatomie et de Physiologie,' 1883, p. 38, pls. v.–viii.

the direction of that region of the brain which, at a later period, is occupied by the conario-hypophysial relics is described and figured, under the term "aditus anterior" and "pharynx primitif" *.

In fig. 5 ("Embryon du poulet de 44 heures"), *a* 1 is the anterior or first ("première") cerebral vesicle; *b* 2, the second cerebral vesicle; *c*, the notochord; *d*, "primitive pharynx."

The branchial chamber, *e*, with the pulsating vesicle and first rudiments of gills, here repeat the branchial sac which

Fig. 6.

receives the oral aperture of the alimentary canal in the Ascidians, a structure which is the condition of the deviation, in a higher step of the Life Series, of the œsophagus from its primary course, and of its communication with the precocious gill-chamber, which then becomes the vertebrate mouth, retaining the closer resemblance to the Ascidian branchial sac in the lowest (piscine) forms of Vertebrata (*Amphioxus*).

In fig. 6 (a longitudinal section of the chick-embryo of 52 hours), the first, 1, and second, 2, cerebral vesicles have expanded and approximated, the interspace is reduced to the

* *Ib.* p. 54.

"pituitary-infundibular tract" below and the "pineal" tract above. The primal fore end of the alimentary canal, *a*, has shrunk, receded, and the communication with the branchial pharynx and subsequent mouth is imminent*.

In Ascidians a pore is formed at the front end of the nervous tube leading into the part which eventually gives rise to the ciliated sac, situated, in the adult, at the junction between the mouth and the branchial sac.

So in *Amphioxus* a mouth, or oral passage, is formed, which opens behind into the branchial or vascular expansion from which the alimentary canal is continued. This branchial sac is on the under or hæmal side of the fore part of the neural axis, issuing, in the lower division of Vertebrates, in the perfection of a water-breathing apparatus, and manifesting in the embryos of the higher half of the subkingdom unequivocal traces of a branchial organization, as shown in fig. 4, 10. But, although this organization subsides, the hæmal mouth, or "tritostome," is in them retained.

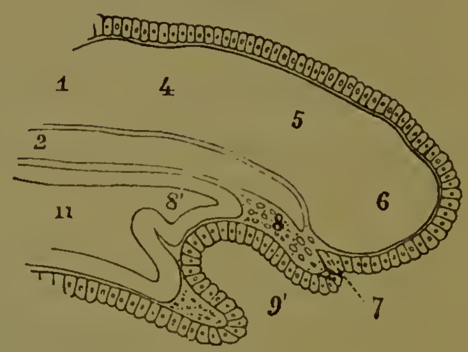
Having noted, briefly, the indications of an earlier or neural mouth-way, or œsophagus, in the embryo of Vertebrates next above the brainless *Amphioxus*, I may premise that, with the appearance, in Invertebrates, of a brain including both supra- (fig. 3, 6) and sub- (*ib.* 3) œsophageal masses or ganglions—better termed, respectively, "hæmœsophageal" and "neurœsophageal"—the canal dividing them is developed as a "gullet" (*ib.* 10), and its outward opening is established as a "mouth" (*ib.* 7) or "deutostome."

In cerebral Vertebrates the beginning, or attempt so to speak, of a canal or tubular extension directed brainward is contemporaneous with the enlargements of the fore end

* Reference may be made to the original 'Mémoire' for the explanation of other letters in the above cuts.

of the myelencephalon, as seen in the embryos of Cyclostomous fishes*. In fig. 7 these enlargements are represented by the figures 4, 5, 6, the latter now pushing beyond the notochord, 2. Toward the middle one of these extends the tubular production (8′) from the digestive sac (11). In the line opposite to the production (8′) is an infolding of the ectoblast (7), which Scott indicates as that of the nasal cavity and hypophysis ("gemeinsame Einbuchtung für Nasengrube und Hypophysis," *loc. cit.* p. 171, Taf. ix. fig. 31, N. H. E.). Beneath this has commenced the wider infolding of the ectoblast (fig. 7, 9′), which, extending backward, and subsequently expanding and developing the branchial sacs, ultimately effects a communication with the alimentary cavity (11), and establishes the permanent oral entry thereto. In the more highly organized cartilaginous fishes (Elasmobranchs) the hæmal permanent mouth, or "tritostome," is also due to involution of the epiblast, forming a sac, beneath the base of the brain, the closed end of the sac coming into contact with the fore end of the alimentary cavity, developing upward the infundibulum. Balfour sees the rudiment of the hypophysis

Fig. 7.



Enlarged scale of a longitudinal vertical mid section of an embryo of *Petromyzon Planeri* at the eighteenth day.

* See Owsjannikow, "Die Entwicklungsgeschichte der *Petromyzon fluviatilis*," Bulletin de l'Acad. Imp. St. Pétersbourg, tom. xiv. 1870, p. 325; Calberla, Morpholog. Jahrbuch, Bd. iii. p. 226; Scott (W. B.), Morpholog. Jahrbuch, Bd. vii., erstes Heft, p. 131, "Beiträge zur Entwicklungsgeschichte der Petromyzonten," from which treatise the subject of fig. 7 is taken.

in a process of the mouth-involution which becomes "constricted off." But he recognizes that the blind anterior end of the alimentary canal—which he terms "throat"—is in close contact with the "pituitary involution." This "involution becomes longer and dilated terminally, while the passage connecting it with the mouth becomes narrower and narrower, and is finally reduced to a solid cord, which in its turn disappears. The remaining vesicle then becomes divided into lobes, and connects itself closely with the infundibulum" *.

In higher Vertebrates the deuto- or pseudo-pharynx (figs. 1, 2, 4, 8), extending to the parts ultimately modified as a pituitary body or hypophysis with its onward and neurad extensions—the infundibulum, third ventricle, and pineal production—constitutes therewith the modified canal which traverses the interspace between the homologues of the Invertebrate "hæmœsophageal" (fig. 3, 6) and "neurœsophageal" (fig. 3, 3) brain-masses—in Vertebrates the fore brain and following brain-parts. In other words, from the neural side of the embryonal or primary buccal cavity a communication (figs. 1–4, 7, 8) is more or less carried on toward the surface from the part where what is a diverticulum from the primitive closed œsophagus (fig. 5, 8′) seems to be seeking, as it were, its outlet at the neural aspect of the body above a wide interspace (fig. 4, 5) now separating the rudiment of the fore brain (6) from those of the mid (4) and hind (3) brains.

In all Invertebrates with appreciable homologues of these divisions of the Vertebrate brain, the neural mouth (fig. 3, 7) is opened at this part, the primordial attempt to attain it in the Vertebrates is fulfilled, and the communication of such

* 'Monograph on the Development of Elasmobranch Fishes,' 1878, p. 190.

neural mouth with the alimentary canal is completed and becomes the persistent gullet (*ib.* 7, 10).

The proposition, therefore, which I now submit is, that the conario-hypophysial tract in Vertebrates is the modified homologue of the mouth and gullet of Invertebrates. That the neur- or subœsophageal ganglion, or ganglionic masses, or neural cords (fig. 3, 3, 5), constituting the centres whence are derived and caudally continued the homologue of the Vertebrate myelon (*ib.* 1), together with the part of the gullet they encompass, are consequently the homologues of the parts of the brain (fig. 2, 4, 3) posterior to the cerebrum (*ib.* 6) and of the ventricle (fig. 4, 5) intervening between the upper and lower ends—pineal (*ib.* 7) and pituitary (*ib.* 8)—of the conario-hypophysial tract. Thus, as it appears to me, is the *Unity of Organization or Composition* vindicated, though in a transitory manner, between the Vertebrate and Invertebrate brain-possessing animals. The foregoing developmental phenomena have mainly guided me to a homological application which, so far as my readings have extended, appears not to have suggested itself.

An obvious difference from the mature Vertebrate is the greater relative proportion, in length, of the encephalic to the myelonic divisions of the neural axis, in the early stages of development, and the retention of such character in degrees corresponding with the low position of species in the Vertebrate subkingdom. It is conspicuously manifested by the relative extent of the interspace dividing the fore brain from the mid brain, depending chiefly on the functional relations of the interposed alimentary canal in Invertebrates (fig. 3, 7-10). The proposed homology appears to me to throw some welcome light on the similar though transitory proportions of the same interspace in the Vertebrate, even the Mammalian, embryo, as exemplified in fig. 4. And we now look with interest

upon the evidences afforded by mature Vertebrates at the lower end of their scale for any retention of this character—a passing one—in the higher forms.

Fig. 8.

Brain of *Chimæra.*

Fishes, especially the cartilaginous, yield such illustrations. I may refer to Busch's descriptions and figures of piscine brains exemplifying such suggestive characters, in his excellent monograph 'De Selachiorum et Ganoideorum Encephalo'*, from which the illustrations of such character in the brain of the Sturgeon (*Acipenser sturio*), and more especially in that of the *Chimæra monstrosa*, are taken, in figs. 173 and 179 of my 'Anatomy of Vertebrates.' The long cord-like lamellæ continued from the optic lobes (fig. 8, 4) to the cerebral one (*ib.* 6), equal in longitudinal extent both mes- and prosencephalon combined. The so-termed "third ventricle" appears as an elongated widely open channel, the side walls of which (*ib.* 5, 5) are thickened and, expanding into the cerebral hemisphere, seem to represent the "crura cerebri." They indicate that these so-called cords or tracts, in Vertebrates, may be homologous with the parial cords or tracts girting the gullet and connecting the fore brain (fig. 4, 6) with the hinder masses (*ib.* 3) in Invertebrates; to which pair of intercommunicating tracts the oral end of the gullet in Invertebrates and the conario-hypophysial tract in Vertebrates hold like relations.

In Birds the primitive œsophageal tube is partially obliterated by ingrowths of a vascular tissue, the folds of which have a branched character, recalling the structure of a choroid

* 4to, 1848.

plexus, but the branches retain a cavity: they are connected by a narrow stalk with the interior of the mid brain. In the section of the brain of an embryo Rabbit 4 centimetres in length, Mihalkovics shows the pineal body projecting behind and above the level of the prosencephalon, and its continuation with the pituitary and infundibular tracts, through the intervention of such modified intermediate portions of the deutostomal tract*.

And here I am inclined to suggest that some cerebral malformations may be viewed in relation to the foregoing transitory evolutional characters.

Malformations from arrested development, included by Geoffroy St.-Hilaire in the 'Mémoires de l'Acad. des Sciences,' and summed up in the 'Philosophie Anatomique,' exemplify phenomena which relate to the space between the fore and hind brains, and which, at such early stages, seem to be associated with the abortive attempt of the alimentary canal to penetrate and traverse such interspace.

In one of the instances given by Prof. Cleland in his interesting "Contribution to the Study of *Spina bifida*, *Encephalocele*, and *Anencephalus*"†, occurs the following:—"The cerebellum is barely recognizable in two lateral parts sundered one from the other." "Projecting forward in the middle line is a hollow pouch about 2 inches long and $\frac{3}{4}$ inch broad, with tolerably tenacious walls, like the finger of a glove. This is the infundibulum and lamina cinerea, and possibly includes the cerebral part of the pituitary body" (or what would have become such if the transcerebral "pouch" had not been arrested). "At the tip of this pouch, in front, one can recognize stretched remains of the optic nerves and some slight vestige of the optic commissure." "On raising the

* 'Entwickelungsgeschichte d. Gehirns,' 1877.

† 'Journal of Anatomy and Physiology,' vol. for 1882, pp. 262, 264.

collapsed roof of the skull, there were first seen two hollow sacs, placed symmetrically, with little cerebral substance in their walls; and between these was found a larger and more thinly-walled pouch projecting forwards, mesially, from the brain behind." "The mesial pouch when floated out in spirit was then seen to have a considerable cavity. Its membranous wall was so thin that it was much damaged in the removal, but the pituitary body adherent to it shows it to be the infundibulum."

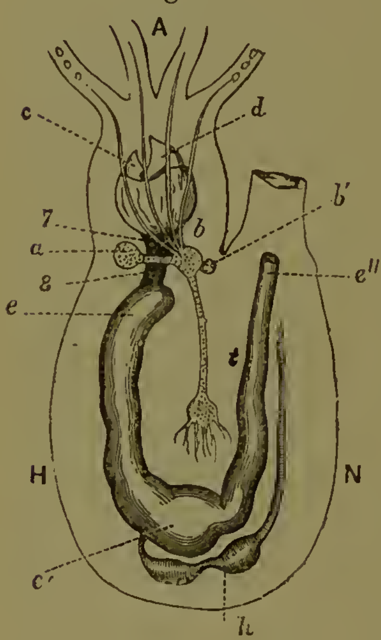
Perception of the homologies above indicated, and researches stimulated by the idea, led to thoughts of their bearing upon the following higher generalization.

At the period of my student's career in Paris the biological mind was exercised by the question of "Unity of Plan" or "of Composition" in the Animal Kingdom as exemplified between Articulates and Vertebrates by reversing the position of the former, and turning what was regarded the under or ventral side of the crustacean or caterpillar upward, as shown in fig. 3, so as to correspond with the upper or dorsal side of the Fish or Quadruped. The alleged "Law" was further elucidated, as between Vertebrates and Mollusks, by bending a quadruped so as to bring the pelvis in contact with the nape, and so parallelling it with a cuttlefish—propositions adopted as demonstrative of their "Unity of organic Plan or Composition" by Geoffroy St.-Hilaire.

To the first of these attempts Cuvier opposed the obvious fact that, though the ganglionic cord of the Articulate might be so brought to the relative position, or place, of the spinal cord of the Vertebrate, yet the chief part of the nervous system, or neural axis, universally recognized as "brain" in both, held opposite relations to the alimentary canal, being above the mouth in the Vertebrate and below the mouth in the upturned Articulate (as is shown in figs. 2 and 3).

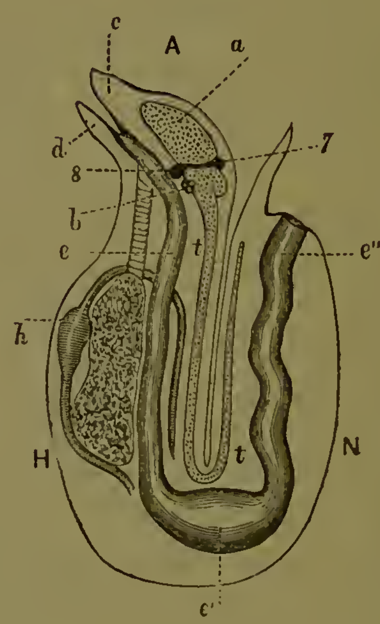
In reference to the second exemplification of the alleged "Unity of Composition," I need only refer to the 'Annales des Sciences Naturelles,' tom. xix. p. 241, pl. xii. (1830), in which Cuvier refuted Geoffroy's conclusions to his own satisfaction and apparently that of the 'Académie des Sciences,' illustrating his argument by diagrammatic views of the organs which he exposed in an Octopus (fig. 9) and in a doubled-up Quadruped (fig. 10). Among other difficulties which he thereby seemed to demonstrate, was the impossibility of making the brain (figs. 9, 10, *a*) hold a corresponding

Fig. 9.



Cuttle.

Fig. 10.



Mammal.

Schematic views as referred to in the text.

position in relation to the alimentary canal (ib. *e*), a fact which was deemed by anatomists of the "Positive School" conclusive as against the "Transcendentalists."

Having satisfied myself that there was a way out of the difficulty by rightly determining the homologies of the mouth

and gullet in Mollusks and Articulates with recognizable structures in Vertebrates, I submitted to my Associates of the Biological Section, D (British Association, 1881), the facts and conclusions which led me to harmonize the oppositions, and to show that the ingenious idea of MM. Laurencet and Meyranx, adopted and advocated by Geoffroy, was not, in point of fact, open to the objection which relegated it to the limbo of exploded notions, where it seems to have rested now for half a century.

I reproduce the diagrammatic illustrations (figs. 9 and 10) by which Cuvier exemplified his objections, in order to show how the homology I have propounded of the "conario-hypophysial tract" affects the argument and conclusion of the great Anatomist. The sole liberty I have taken with that diagram (fig. 10) is to add to the brain of the Mammal the tract in question (7, 8); the significance of which to his argument Cuvier as little suspected as have his successors who have devoted time and thought to the higher generalizations of Biology.

After demonstrating, by reference to the Badger, that colour does not indicate the back of an animal, Cuvier proceeds to affirm that naturalists have for the recognition of that aspect a more certain character, viz. the position of the brain:—"Ils ont pour reconnaître les dos un caractère plus certain : c'est la position du cerveau"*.

Now, by the term "cerveau" Cuvier does not here mean the sum of neural expansions usually called "brain," but only one of them, that, viz., which he indicates (as in figs. 9 and 10) by the letter *a* in both Cephalopod and Mammal; it is the part which is termed the "supraœsophageal mass, ganglion, or pair of ganglions" in Invertebrates, and the

* *Tom. cit.* p. 251.

"cerebrum" or "cerebral hemispheres" in Vertebrates. It is divided, as already remarked, from the "subœsophageal ganglions," completing the totality of the brain in Invertebrates (fig. 3, 3, fig. 9, *b*), by the extension of the gullet and mouth to the aspect of the body which bears relation to, or corresponds with, that of the main centres of the nervous system—such centres answering, as to the parts they supply and, in Articulates (fig. 3, 1), in their continuous extent, to the myelon (fig. 3, 1) and ep- mesencephalon (fig. 2, 3, 4) in Vertebrates. This homology, however, Cuvier did not admit; and herein he has had the support of later anatomists. With respect to the myelon—"moëlle épinière"—marked *t t* in his diagram*, he expressly states that it is peculiar to the type of structure exemplified in his figure A (fig. 10) (of the Quadruped)†. But no evidence is adduced against the homology of the elongate moto-sensory tract, or neural axis, in Articulates, and the elongate moto-sensory but seemingly non-ganglionic tract, or neural axis, in Vertebrates, save their different relative positions in a standing or walking Badger or Beetle. Cuvier assumed, as Gegenbaur and other anatomists have done, that the surface or aspect of the body in progressive motion determines the homology of such surface, and that the surface nearest to which lies the neural axis in Articulates answers to that which is furthest from such axis in Vertebrates. But there are both Vertebrates and Invertebrates in which, during progressive motion, neither the neural nor the hæmal surface is downwards or next the earth.

The subœsophageal mass or ganglions in Cephalopods send

* *Tom. cit.* pl. xii.

† "*t t*, la moëlle épinière propre au Mammifère," *tom. cit.* p. 257 (referring to his subject as a representative of a Vertebrate animal).

off the nerves to the prehensile arms, and are in communication with the viscera, the muscles, and the soft parts of the trunk. Moreover, in Vertebrates this epencephalic homologue is in direct nervous communication with the organ of hearing (fig. 9, *b′*, and fig. 10, *b*). The fore brain, on the opposite side of the gullet in the Cephalopod (fig. 9, *a*), supplies the nervous masses subservient to the large and complex organs of vision, and also parts which may exercise the sense of smell. But, if the subœsophageal mass and the moto-sensory neural continuations of the trunk, *t*, be, in the Cephalopod, homologous with those in the Insect (fig. 3, 1) and Crustacean, the ground on which I predicate, in the Articulate, of the neural aspect of the body, that it answers to that commonly called "dorsal" in Vertebrates, is applicable also to the Mollusk, fig. 9.

Therefore the part which Cuvier indicates in his diagram, and terms brain ("cerveau," *a*), is not a true criterion of the back ("dos"); it occupies in the Cephalopod and other cerebral Invertebrates the aspect of the belly, or tract of the body which I term "hæmal," and which is called the ventral or under part.

To be sure this cannot be predicated of the brain ("cerveau," *a*) of the quadruped. And why? Because the alimentary tract and outward anterior opening which would demonstrate its holding a position opposite to that of the rest of the nerve-centres has been atrophied, and exists as an arrested residuary embryonal part (figs. 3 and 10, 7-8). It is the superadded respiratory organization in connexion with the oral end of the alimentary canal and the concomitant opening of the mouth in a new position, in the Vertebrate, which turns the cerebrum to the side occupied by the rest of the nerve-centres—in other words, to the neural aspect of the body. Individual development being achieved, the Ver-

tebrate becomes "hæmastomous," the Invertebrate remains "neurostomous."

At the embryonal stage of the higher subclass at which the primary mouth was continued across the brain, the "Unity of Plan" between the Vertebrate and Invertebrate animal was exemplified; and that "unity" is, in the main, preserved under the recognition of the neural and hæmal aspects of the body, as shown in figs. 2 and 3, representing the Articulate and Vertebrate types.

In the view of the homologous surfaces of the Invertebrate and Vertebrate bodies as determined by that which may happen to be the upper surface in horizontal station and progression, which surface is accordingly termed "dorsal," the opposite or under surface being "ventral," the chief nerve-mass in the Articulate (fig. 3, c), called "cerveau" by Cuvier, poses as the homologue of the brain in the Vertebrate; and not only so, but being the only part of the central nerve-mass which is "dorsal" in position, or "above" the alimentary canal, it might be entitled, according to the above homology of the body-surfaces, to be the homologue of the entire central nerve-mass (my "myelencephalon") in Vertebrates, which is also "dorsal;" while the ganglionic nerve-cords in Articulates would be in the opposite homological category.

Accordingly the accomplished Anatomical Professor at Heidelberg, in logical concord with such determination of homologous surfaces, holds the so-called "supraœsophageal ganglion" of the Articulate to be, or to represent, the whole myelencephalous tract in the Vertebrate. With Gegenbaur, as with Cuvier, the "spinal cord" is therefore peculiar to Vertebrates, being "dorsal" in position; it bears no true homology with the so-called "ventral" cords, whether ganglionic or not, in Invertebrates.

Dohrn *, while admitting the homology or equivalency of the supraœsophageal ganglions, subœsophageal ganglions, and under or ventral cords therefrom continued, whether ganglionic or otherwise, in Annelids and Arthropods, with the myelencephalous tract in Vertebrates, notwithstanding the opposite sides of the body which they seem to hold, has recourse to ideal ancestral forms in order to reconcile the differences as to relative position shown by the actual or modern subjects †.

Whilst the aspect of the body in connexion and communication with the umbilical vesicle was held to be on opposite sides in Vertebrates and Invertebrates, a strong argument was afforded to objectors to any ascent of the lower to the higher division of animals. So the accomplished Professor of Palæontology, in the 'Muséum d'Histoire Naturelle,' Paris, writes :—"Il importe toutefois de faire remarquer que l'idée de faire descendre les Vertébrés des Invertébrés n'est raisonable qu'à la condition de supposer dans les temps anciens des animaux sans vertèbres organisés autrement que ceux d'aujourdhui ; car il y a des différences profondes entre les Vertébrés et les Invertébrés. A l'époque actuelle, les poissons ont des cartilages, des os en phosphate et carbonate de chaux, leur vésicule ombilicale se continue avec le ventre ; tandis que les crustacés ont de la chitine, n'ont pas de cartilages, n'ont pas de phosphate de chaux, et se développent en ayant la vésicule ombilicale sur le dos" ‡.

My contention is that the true grounds for determining the homology in question are not the positions of the body

* 'Ursprung der Wirbelthiere,' &c.

† I concur with the remarks by Balfour (*loc. cit.* p. 17) on Dohrn's hypothesis, and deem any other objection superfluous.

‡ 'Les Enchaînements du Monde Animal dans les Temps géologiques,' par Albert Gaudry (8vo, 1883), vol. i. p. 249.

which may be assumed by the living animal, but the relative positions to such body of the central parts of the nervous and vascular systems, which relations I have expressed by the terms "neural" and "hæmal." The convenience of these terms or signs is exemplified by the trouble, not to say perplexity, which arises when characters, or developmental phenomena, as of the umbilical vesicle, repeated in Vertebrates and Articulates, are endeavoured to be expressed or expounded on the "dorsal" and "ventral" homological hypothesis.

Balfour, for example, in his keen and accurate views of the primary growths of the myelon, in Elasmobranchs, traces the formation of the central cavity by the "dorsal" folding of the lateral halves of the primitive open canal, which includes the grey matter and carries in also a fold, now become the lining of the cavity, of the embryonal ciliate epiderm.

The primal nerve-roots are, or are attached to, free margins of the dorsal folds, and become the "dorsal," or, in anthropotomy, the "posterior" roots of the spinal nerves. The white matter of the myelon becomes external and lies in greater proportion along the under, or ventral, or anthropotomically "anterior," part, than on the "dorsal" part of the myelon.

Now comes the difficulty arising from the non-appreciation of the homology of the conario-hypophysial infundibular tract with the annulose gullet. "The transverse section of the ventral nervous cord of an ordinary segmented Annelid consists of two symmetrical halves placed side by side. If by a mechanical folding the two lateral halves of the nervous cord became bent towards each other, while into the groove between the two the external skin became pushed, we should have an approximation to the vertebrate nervous system." . . . . "If this folding were then completed in such a way that the groove, lined by external skin and situated between the two lateral columns of the nervous system, became converted into a canal,

above and below which the two columns of the nervous system united, we should have in the transformed nervous cord an organ strongly resembling the spinal cord of Vertebrates"*. But a resemblance, however strong, between the two parts or organs is not, of itself, a ground for predicating homology. For, as the accomplished developmentalist proceeds, "It is well known that the nerve-cells are always situated on the ventral side of the abdominal nerve-cord of Annelids, either as a continuous layer, or in the form of two or, more usually, three bands. The dorsal side of the cord is composed of nerve-fibres or white matter. If the folding I have supposed were to take place in the Annelid nervous cord, the grey and white matters would have very nearly the same relative situations as they have in the Vertebrate spinal cord. The grey matter would be situated in the interior and line the central canal, and the white matter would nearly surround the grey. The nerves would then arise, not from the sides of the nervous cord as in existing Annelids, but from its extreme ventral summit"†.

Parts of the important organs "spinal marrow" and "abdominal cords," ganglionic or otherwise, would doubtless hold the same relative situations in an abstract view of the structures, irrespective of their assumed relative positions in the Annulate and Vertebrate bodies; but in relation to the accepted position of the nerve-centres in the two groups they would hold opposite relative situations in and to the body; the extreme summits of the primitive folds giving origin to the nerves would be dorsal in the Vertebrate, and ventral in the Annulate modifications of the animal structures.

Obliterate the mouth and part of the alimentary canal dividing the fore brain from the hind brain in Annulates, and

* Balfour, *op. cit.* p. 165.

† Ibid.

the parts of the homologue of the myelencephalon (" cerebro-spinal tract" or abdominal nerve-cord) become wholly on the neural aspect of the body, as in Vertebrates. In both divisions the infolding of the side walls completing the central canal occurs on the neural side. In both the nerves arise from the neural summits of such infoldings; and in both the "external skin" would pass from the neural side of the groove into the central (then becoming) ciliate canal. In both the hæmal side of the cord would manifest an excess of the "white matter;" and this with the opposite predominant grey matter would present not "very nearly," but the very same relative positions to the body of the animal containing them (compare figs. 2 and 3).

Of these propositions, the base or support is the homology of the pineal, third ventricular, infundibular, pituitary residuary modifications in the Vertebrate brain with the persistent functional canal traversing the homologous tract in the Annulate or Articulate brain*.

As animals descend in the scale, the instinctive or reflex actions of the nervous system predominate over those that are "willed," or the voluntary actions.

* I have elsewhere ('Archetype of the Vertebrate Skeleton,' 8vo, 1848, p. 2) pleaded in favour of single substantive "terms" in place of "descriptive phrases," and may here cite, as synonyms of "myelencephalon"—"nervous system" (p. 165), "cerebro-spinal nervous system" (p. 99), "central nervous system" (p. 100), "nervous part of the brain and spinal cord" (p. 100); again, as synonyms of "myelon"—"spinal marrow," "spinal cord," "abdominal nerve-cord" (p. 165), "Annelid nervous cord" (*ib.*); also, as synonyms of "myelonal canal"—"medullary canal" (p. 128), "neural canal" (p. 100), "central canal of the nervous system," equivalent to "myelencephalous canal;" "spinal canal" (p. 99), which, in surgery, is a synonym of "vertebral canal." The pages here quoted refer to the 'Elasmobranch Fishes' of Balfour.

In both Vertebrates and Invertebrates, as a rule, the parial limbs diverge from their arches nearer the neural than the hæmal sides of the trunk—nearer to the centres whence their nerves originate. In Vertebrates the joints or segments of the limbs bend toward the hæmal aspect; in Invertebrates they bend from the hæmal aspect: and thus the most frail and precious of the organic systems, namely the neural axis, is brought in Arthropods towards the least exposed and safest surface of the body, that, viz., which is downward, next the ground—therefore called the "belly," or ventral surface or aspect. When the myelencephalous tract runs along the most exposed, dorsal side, it receives an immediate protection by a vertebral column. But the surfaces or aspects of the body which are truly homologous in the Snake and Caterpillar are the *neural* and the *hæmal*, not the *dorsal* and the *ventral*.

CHAPTER II.

CEREBRAL HOMOLOGIES IN VERTEBRATES AND INVERTEBRATES.

In a study of the homologies of the Divisions of the Vertebrate brain with Nerve-centres in Invertebrates, the subjects of comparison should be the best-developed anterior and special-sense masses in the latter and the least-developed ones in the former subkingdom.

In many Fishes—*Lepidosteus, Anguilla,* e. g.*—the neural masses in direct relation to nerves of special sense are as large as, or larger than, those not so related bearing the names of "cerebrum" and "cerebellum," these being the homologues of those centres which receive, in higher Vertebrates, such vast accessions of grey and white neurine as to represent, or seemingly compose, the whole organ known as the "brain" in man and most mammals.

The chief accumulation rises and expands from the parial nerve-tracts or "crura" between those portions of the tracts which, in front of the cerebral hemispheres, develop the masses or ganglia related to the sense of "smell," and those behind the hemispheres related to the sense of "sight." Next in retral succession are enlargements related to the sense of "taste" and to movements of parts of the mouth; behind the "trigeminal" centres are those subserving the sense of "hearing;" above these centres rises the "cerebellum."

Thus the central masses of the neural axis in relation to the "special senses" run in longitudinal sequence from before

* 'Anatomy of Vertebrates,' 8vo, vol. i. (1866), p. 275, figs. 174, 175.

backward, and might be called the "ganglions" of smell, sight, taste, and hearing.

These several sense-centres are not in contact with one another in all Vertebrates. The olfactory ganglia are connected by long cords with the optic ganglia in many fishes (Cyprinoids *e.g.**). The tracts intercommunicating with the trigeminal lobes recall the corresponding ones known as "œsophageal cords" in Mollusks and Insects. Short and thick in all Vertebrates are the tracts of the macromyelon, or "medulla oblonga," connecting the gustatory with the auditory nerve-centres; but all such centres, with superadded masses, are reckoned parts of the "brain."

The condition which affects the length and tenuity of the tracts connecting the optic (diagram, fig. 11, *a f*) with the oral (ib. *b*) nerve-centres in Invertebrates is the course of the alimentary canal (ib. *c l*) neurad †, along the interspace between the foremost and the next neural centres.

The elongated homologues of the vertebrate "crura cerebri" are termed by Lyonnet, with sound homological views, "conduits de la moëlle épinière" ‡; by later anatomists, rejecting his views, "œsophageal cords" or "commissures."

In illustration of the present suggestions of the homologies in question, I propose to take, from the group of Arthropods, the nervous system of the Locust §.

The first, commonly foremost neural mass (fig. 11, *a*),

* *Tom. cit.* p. 275, figs. 177, 178.

† Ibid. p. 276, fig. 172 (*Chimæra*). See also *ante*, fig. 3.

‡ 'Traité anatomique de la Chenille qui ronge le bois du Saule,' 4to, 1762.

§ As represented in *Caloptenus femur-rubrum*, *C. spretus*, and *C. bivittatus*, by the exemplary dissections and microscopic sections of MM. Burgess and Mason, described and figured by Prof. Packard in the 'Second Report of the U.S. Entomological Commission,' 1880, pp. 223–242, pls. ix.–xv.

which, by the course of the œsophagus, *c*, in Mollusks and Articulates, is turned to the hæmal aspect of the alimentary canal, is that which is usually designated the "supraœsophageal ganglion," or, after Lyonnet and Cuvier*, "the brain."

This consists of a pair of neural masses, or "hemispheres," confluent mesially for one half of their longitudinal extent, before and behind which confluent tract they are free. Each moiety presents three lobes or enlargements, the smallest of which receives the antennal nerve (fig. 11, *e*), a second, the largest, the optic nerve, *f*, the third the ocellar nerve, *g*†. From the œsophageal surface of each moiety proceeds the tract or "commissure," *d*, which, traversing its own side of the gullet, converges to and, with its fellow, expands into the neural mass termed the "subœsophageal ganglion," *b*.

With this neural mass are connected by origin or insertion the nerves, *h*, *i*, of the "trophi," *i. e.* the labrum, the mandibles, the maxillæ, the labium with its tongue-like extension, and the sense-organs called "maxillary" and "labial palpi," together with the complex muscles of these several parts.

The properties of the vertebrate mouth, viz. taste and motions, may be reasonably assigned to the foregoing invertebrate oral organs: accordingly the nerves connected therewith, endowing the mouth with the same characteristic powers and properties for testing, seizing, and comminuting alimentary substances, I deem, with their neural centres, to be homologous with those of like endowments in the vertebrate animals.

* "Le cerveau proprement dit," Leçons d'Anat. comparée, ed. 1845, tom. iii. pp. 305, 335.

† I omit the filaments connecting the foremost minute mesial ganglion of the "sympathetic" or "stomato-gastric" system with the above cerebral mass.

The part of the vertebrate brain to which, therefore, the so-called "subœsophageal ganglion" in Invertebrates is analogous and, I conceive also, homologous, is the basis of the epencephalon known as the "medulla oblongata" (macromyelon), or so much of that myelencephalous tract as may be in connexion with the trigeminal and hypoglossal nerves—the neural machinery, to wit, for the sensations and motions of the parts forming or being lodged within, or furnishing secretions to, the vertebrate mouth.

Through the different course of the gullet, in relation to certain nerve-centres in Vertebrates and Invertebrates *, a greater degree of juxtaposition and concentration of those centres connected with the special senses, and the neural mechanism relating to the reception of their impressions, is possible in the group in which the "brain," or sum of such centres, is not traversed by the alimentary canal.

We are thus prepared for the conception that, as the oral nerve-centres in Invertebrates are so far removed from the narial nerve-centres, so the ear-organs and their centres may be correspondingly remote from the oral ones.

Johannes Müller recognized a structure in the fore leg of the *Gryllus hieroglyphus*, which von Siebold detected in other Orthoptera; and this structure was by both regarded as the true seat of the auditory sense. The vesicle, in connexion with a *quasi* tympanic membrane closing an orifice in the fore leg, receives two unusually large nerves from the foremost "thoracic ganglion" (fig. 11, *o*); these nerves accompany the tracheal branch of the vesicle; the lesser nerve attaches itself to the vesicular dilatation, and there expands into a flattened tract, displaying a structure akin to that of the acoustic nerve lining the semicircular canals in Vertebrates. This inter-

* *Ante*, pp. 8 and 9, figs. 2 and 3.

pretation is accepted by the experienced anatomist of the Arthropoda, Prof. Packard, who writes:—"In the green Grasshoppers, such as the *Katydes* and their allies, whose ears are situated in their fore legs, the 'first thoracic ganglion' is a complex one" *, such "auditory nerves" communicating therewith.

Although, physiologically, the remoter neural mass may be compared with the part of the epencephalon in connexion with the auditory organ, it may be too much to look for consent to a corresponding homology. And, if such be denied, yet the retral transfer of a sense-character beyond the gustatory one to the foremost or even a remoter thoracic nerve-mass may not, consequentially, affect the grounds for homologizing both the so-called "supra-" and "subœsophageal" ganglia, which are constant in regard to their special sense-nerves, with the parts of the vertebrate brain similarly distinguished by relations to nerves of special sense.

Conclusions counter to these homologies either limit the term "brain" to what is called the "supraœsophageal ganglion" in Invertebrates, or, more consistently, involve a negation of the homology of any part of the central neural system in Invertebrates with any part of that system in Vertebrates.

The latest neurotomist of the Arthropoda, for example, concludes, emphatically, as follows:—"It should be remembered that the word 'brain' is applied to the compound (supra-œsophageal) ganglion simply by courtesy and as a matter of convenience, as it does not correspond to the brain of a vertebrate animal, the brain of the horse or man being composed of several distinct pairs of ganglia. Moreover, the brain and nervous cord of the fish or man is fundamentally different,

* Packard, 'Second Report' &c. p. 225.

or not homologous with that of the lower or invertebrate animals." "The nervous cord of the insect consists of a chain of ganglia connected by nerves or commissures"*.

The "nervous cord" here signifies the central tracts—ganglionic or otherwise—occupying in Invertebrates what is held to be, and is described as, the "ventral region" of the body-cavity.

The structural phenomena cited in support of the foregoing negation are:—"The entire brain of an insect is white, as are all the ganglia" †; while "the spinal cord of the fish or man consists of two kinds of substances or tissues, called 'grey' and 'white' substance" ‡.

But the associated microscopical investigators and manipulators, Burgess and Mason, found in the "entire brain" (my "fore brain," or "hæmœsophageal centres," *a*):—"I. An outer, slightly darker, usually pale greyish-white portion, made up of 'cortical cells'" §; and "II. The medullary or inner part of the brain consists of matter which remains white or unstained after the preparation has remained thoroughly exposed to the action of carmine. It consists of minute granules and interlacing fibres. The latter often forms a fine irregular network enclosing masses of finely granulated nerve-matter" §.

Remembering the transposition of the grey and white neurine in different parts of the vertebrate neural axis, I cannot give the value to a similar transposition in parts of the invertebrate neural axis which Professor Packard assigns thereto.

The eyes of the Cuttlefish are the homologues of those of the Lump-fish, as are the optic nerves and the cerebral mass

* Packard, 'Second Report' &c. p. 224.
† Ib. p. 224. ‡ Ib. p. 226.
§ Ib. p. 227.

superadded, in both, to the centre receiving the impressions of those nerves. Such homology legitimately extends from Cephalopods to the Invertebrates in which a homologue of the vertebrate hemispheres may not be so largely developed or superadded.

Accordingly I conclude that the collective neural centres and their intercommunicating tracts in Invertebrates are the homologues of those centres and tracts called "brain and spinal cord" in Vertebrates, and that such "neural axis" marks, in both grades of the animal series, the same position in the body, and the same local relations to the vascular centre, *m*, and the alimentary canal (fig. 11, *l*). As a corollary, the neural axis, or "ganglionic cord" in Arthropods (*b o n*) denotes the neural position, and supports the inference that its foremost portion, *a*, is simply displaced by the course of the gullet through the brain in order to open by a mouth upon the neural aspect of the body (as in fig. 3). The suppression of such transcerebral tract in Vertebrates allows the continuation of the alimentary canal forwards to an oral opening on the hæmal aspect of the body (as in fig. 2). Here the œsophagus offers no obstacle to the approximation of the main cerebral centres to each other—the fore brain to the hind brain. Hence that juxtaposed allocation of the primary encephalic divisions, associated with the progressive accumulations of grey and white neurine, which the cerebrum and cerebellum present, in relation to the centres subservient to the ingoing conductors of sensations and the outgoing ones of motions, as we pass in their contemplation from the fish to the ape and the man.

The so-called "brain" in the Locusts answers to a part only of the brain of a fish; moreover it is not a "supraœsophageal ganglion," but a "sub-" or "hæmœsophageal" one

The next neural mass in the brain of the Locust (*b*)

answers to the epencephalon of the fish; it is not a "sub-œsophageal ganglion," but a "supra-" or "neurœsophageal" one, and the foremost of that series of the neural centres or "ganglions."

The homologue of the vertebrate myelon in Invertebrates is not protected by a special bony case or "vertebral column." The "ganglionic cord" is nevertheless the most precious, as it is the most delicate and crushable of an insect's organs. Hence it has been, so to speak, ordained that the part of the body's surface to which the neural axis is nearest should not be, as in the beast, along the part most exposed and liable to blows. By a modified flexure of the limb-segments the trunk of a beetle or lobster is turned so as to hold the same relative position to the ground as does the part of the beast's body least exposed to injuries.

The aspects of the trunk in locomotion are no primary or essential characters of a natural group. Some insects, indeed, swim with their neural surface upwards, as does the fish.

Active *Bimana*, in the aspects of the trunk, differ from both beasts and beetles: when a man stands, his body is at right angles to the ground, and the limbs are in the same line with the trunk. But the heart in man indicates the "hæmal" aspect, the myelon the "neural" aspect, as in the animals of lower grade, whether vertebrate or invertebrate.

The restriction by Cuvier of cerebral homologies to the so-called "supraœsophageal ganglion" in the latter zoological division leads me to add a few remarks on what may be derived from the molluscous subkingdom in illustration of my present subject. In this group, indeed, the great anatomist admitted an exception in favour of the highest Cephalopoda*.

* *Op. cit.* tom. iii. p. 297.

In fact, the encephalon in the Dibranchiate order resembles that of Vertebrates in the mutual proximity of the "fore" and "hind brains" (fig. 9, *a b*); so approximated, they are both also protected partially by a cartilaginous case which, with some histological modification, is analogous to, if not homologous with, the vertebrate cranium.

But the cephalopodic brain retains the invertebrate condition of giving passage to the gullet along the tract or part answering to the third ventricle and thalamencephalon; only the lateral boundaries or crural tracts are much shorter and thicker than in inferior Mollusks or in Articulates.

Still it is plain that the nervous mass on one side of the gullet answers to the so-called "supracœsophageal ganglion" (fig. 3, 6), and that on the opposite side to the "subœsophageal ganglion" (ib. 3) of lower Invertebrates.

The latter centre, in Cephalopods, sends off the acoustic nerves (fig. 9, *b'*), and is continued into the cords, *t*, which endow the muscles and skin of the trunk with the motory and sensory powers. A closer resemblance than is usually seen in Invertebrates to the Vertebrate myelon is moreover manifested by the conspicuous ganglions developed on the sensory tracts or cords of the trunk*, and the non-ganglionic continuation of the motory division of the body-cords continued from the Cephalopod's brain.

From the beginning of the short and thick side-tracts which indicate, if they do not represent, the parts of the vertebrate brain intervening between the "pros-" and "epencephalon" the optic nerves are given off. I need not repeat their well-known characters and developments in relation to the large and complex eyes of the Dibranchiates.

Beyond the origin of the optic nerves each side-tract termi-

* 'Anatomy of the Pearly Nautilus,' 4to, 1832, p. 37, pl. 7. fig. 3.

nates in a "subœsophageal" mass, divided into two portions and supplying the parts corresponding with those in Vertebrates which send and receive their nervous influences through the "medulla oblongata" (macromyelon) and the "spinal cord" (myelon).

The dibranchiate homologue of the supraœsophageal ganglion moreover supports a part of the vertebrate cerebrum, less manifestly, if at all, shown in other Invertebrates. It is a superposed mass of a whiter colour than the rest of the encephalic centres, with an indication of a division into a lateral pair of lobes, and, in *Sepia*, presenting a subtriangular form with the apex anterior. From the deeper-seated part of the "supraœsophageal" mass are sent off, besides smaller filaments, a pair of nerves, or "crura," which converge and are lost in a more anterior ganglionic mass—the "ganglion sus-buccal," or the superoral ganglion, of Cuvier—which distributes nerves to the delicate membranous folds and processes developed from the interspaces of the cephalic arms, and to the plicated and papillose lips which surround and project anterior to the beak, and which soft and lubricous parts we may reasonably suppose to receive from their supraœsophageal, or cerebral, centres the faculty of judging of the odorous qualities of the substances to be seized by the beak.

From the anterior portion of the larger "subœsophageal" mass are sent off nerves to the rasping and gustatory organs within the mouth, and the larger nerves which supply the eight cephalic acetabuliferous arms and tentacles. From the posterior division of the subœsophageal mass are sent off the moto-sensory nerves of the trunk already noticed, and also visceral nerves*.

In the Tetrabranchiate Cephalopods the foregoing primary

* 'Anatomy of the Pearly Nautilus,' 4to, 1832, p. 38, pl. 7. fig. 3.

divisions and functions of the brain are simplified, and so are more clearly manifested. The cartilaginous defensive case protects only the homologue of the "sub-" or, rather, "neur-œsophageal" ganglion, which is more distinctly divided into a fore and hind mass. The first of these supplies the anterior or cephalic muscular and tegumentary parts, the second the posterior or corporal ones; and from this division or cerebral centre are derived the nerves of the acoustic organs developed or imbedded in the corresponding supporting cartilage*.

The super- (hæm-)œsophageal body develops no peripheral lobe, is in the form of a thick cord which sends forward nerves to oral parts suggestive of an olfactory function, and, laterally, the large short cords, swelling into ganglions, subserving the retinal supply of the pedunculate eyes.

The brain-space traversed by the gullet is wider than in the Dibranchiates, the annectant tracts between the "supra-" and "subœsophageal" masses are longer; but their resemblance to the œsophageal cords in the Articulates is still closer in the modifications of the cephalopodal type of the nervous system, especially of its encephalic centres, which are seen in *Aplysia* and all lower Mollusca.

John Hunter, in his descensive comparison of the brains of animals, stopped at the Snail. In my description of these Preparations I quoted from the scrap of manuscript which he had attached to the numbers of the preparations and names of the dissected animals. Being arranged in the ascending series, the MS. begins:—"The First Class has a brain in the form of a ring, through which passes the œsophagus. It consists of a pulpy substance, somewhat transparent, which is

* Macdonald, "Anatomy of the *Nautilus umbilicatus*," Phil. Trans. 1855, p. 279.

easily squeezed out when the brain is cut into. It is not inclosed in hard parts, and is not defended from pressure or injuries more than any other part." ('Physiological Catalogue,' 4to, vol. iii. p. 4, 1836.)

Balfour* deems the nerve-cords in *Peripatus* and the primitive molluscan type *Chiton* to be the circumoral ring longitudinally extended.

For the further development of this part of Comparative Anatomy, I need only to refer to the rich series of Monographs for which we are indebted to Mr. Robert Garner, F.L.S., of Stoke-upon-Trent†, still in enjoyment of health and intellectual vigour; also to another, whose loss we lament, the late Dr. Albany Hancock, F.R.S.‡

In his admirable researches on the Nervous System of Insects, Newport§ discovered that "the nervous cords between the ganglia included two columns," and that "the *inferior* column alone goes to the formation of the ganglia, whilst the *superior* lies upon them without any perceptible enlargement." Upon this he founded his distinction of the "motor" and "sensitive" columns in Insects as in Vertebrates. This, of itself, must weigh in the question of the homology of the ganglionic cords of Articulates with the myelon of Vertebrates; and acceptors of such homology gain by a determination of the corresponding surfaces of the entire frame in the two groups. If the ganglionic cord be the homologue of

* 'Comparative Embryology,' 8vo, 1881, vol. ii. p. 312.

† See his beautifully illustrated memoirs in the Transactions of the Linnean Society, vol. xvii. (1837), and in the Transactions of the Zoological Society, vol. ii. (1835).

‡ By monographs in the publications by the Ray Society, in the 'Annals of Natural History,' and in the 'Philosophical Transactions,' with his associate workers Embleton and Alder.

§ 'Philosophical Transactions,' 1843, p. 243.

the myelon, the surface of the body next to which those nerve-centres are respectively extended must be the same. If such surface be turned downward in the ordinary station and progression of an Insect, the columns on which the sensory ganglions are formed will be "inferior;" while in Vertebrates, according to the position in which the body may be carried, the ganglionic or sensory columns will be "superior" in the beast and "posterior" in the man. Terms, therefore, defining aspect and position independent of the accident of limb-direction, should be acceptable: "neural" and "hæmal" are as applicable to parts as to wholes.

A heart, whether compact or elongate, has a surface looking toward the neural aspect, and a surface with an opposite aspect. One may predicate of the hæmal side of a "heart" or "dorsal vessel" whether it be at the fore side of the body (in a man), or at the under side (in a beast), or along the upper side (in an insect). So likewise with regard to the nervous axis: Newport's sensory ganglions in that of the Insect are developed in and from the cords on the "neural" side of such axis, as they are in the "neural" columns of the Vertebrate myelon, as distinguished from the "hæmal" columns.

Developmental researches may gain by such appreciation. The admirable Investigator whose recent loss Morphologists deplore, thus writes:—"The embryo of *Peripatus* shows what was once part of a continuous slit running nearly its whole length;" . . . "it at first leads into the alimentary canal, like the neurenteric canal of the vertebrate embryo; but this communication is closed prior to the appearance of the first rudiments of the ventral nerve-cords"*.

* *Op. cit.*

The primitive streak, or slit, prior to its closure as the medullary canal, occupies the same position or aspect of the body in the vertebrate embryo as does the so-termed *ventral* position in *Peripatus*—that, namely, which in Vertebrates is called "*dorsal*" as arbitrarily as in Invertebrates it is called "*ventral*." It is the homologous aspect or position of the body in both.

But, to resume, my contention here is, that the homologues of the primary divisions of the brain in Mollusks are the parts known in Articulates as the "supra-" and "sub-œsophageal ganglions" with their commissural or annectant cords or "crura," that the topical relations of these parts to the gullet are the same in both great divisions of Invertebrates, and that the homologies of the aforesaid parts with the primary divisions of the Vertebrate brain are affected solely by the altered relation thereto of the gullet and mouth.

The homologies of the Dibranchiate brain, notwithstanding the œsophageal and oral differences and a non-appreciation of their essential nature and cause, were recognized and affirmed by the Father of the anatomy of the Mollusca. They are clearly expressed in the first of his immortal 'Mémoires'* on that subject; and are briefly summarized in the 'Leçons d'Anatomie comparée.' After describing the "sub-" and "supraœsophageal" centres, Cuvier affirms:—"On pourrait comparer le premier au cervelet, l'autre au cerveau des Vertébrés." If for "cerebellum" one writes "epencephalon," this defined correspondence of the brain of the highest Mollusks with that of the lowest Vertebrates would square with my own convictions.

* 'Mémoires pour servir à l'Histoire et l'Anatomie des Mollusques,' 4to, 1816, Mém. 1[er], "Sur le Poulpe (*Octopus vulgaris*)."

But now I am driven to ask, Why did Cuvier refuse to extend his views, whether homologieal or analogieal, of the answerable parts of the brain in Vertebrates and Invertebrates beyond the "supracœsophageal" mass or ganglion in Mollusks and Artieulates? Beeause, unlike Hunter, he declined to extend those views in relation to the Vertebrate and Invertebrate encephalic centres beyond or below the higher order of Cephalopoda; and he logieally pronounced, at the eonelusion of his admirable anatomieal monograph of the "Poulpe" (*Octopus vulgaris*), that the elass of whieh it was the type—my Cephalopoda Dibranchiata—formed not the passage to any other group, and that they have not resulted from the development of other animals, and that their own development has produced nothing superior to them*. It must be remembered, however, that the transitional modifications of the Tetrabranchiate Cephalopods had not at that date been made known.

If, however, the eerebral homologies may be traeed, with the guidanee of the Pearly Nautilus, through the still lower, more simplified Mollusca, notwithstanding their retaining more of the lower and primitive eircumoral type, my next contention is that those homologies may be predieated of the modifications of the brain in the Artieulata.

So plain, so obvious, indeed, seem to me the grounds for sueh homologies, that I should have shrunk from urging them before my fellow-labourers in Zootomy were not views very analogous to the restrieted ones of Cuvier maintained and asserted by the aceomplished and experienced eomparative anatomist, especially of Invertebrate animals, in the United Sates, to whose valuable Monograph † I have already referred.

* 'Mémoire sur le Poulpe,' *op. cit.* p. 43.

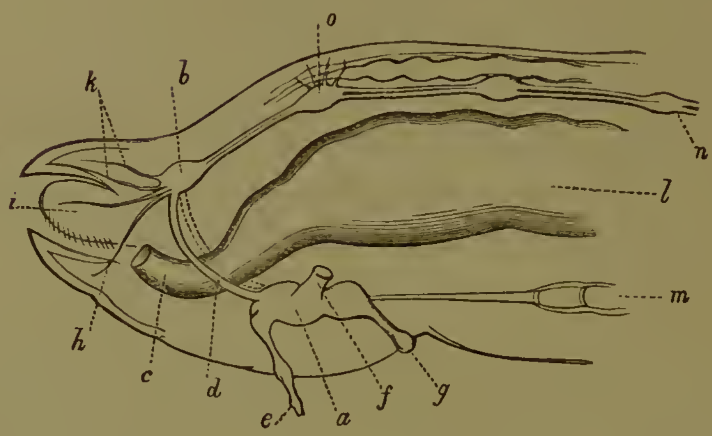
† *Ante*, p. 33.

I gladly, however, welcome the authority of the indefatigable Dissector of the Mollusca in predicating corresponding parts of the nervous centres in the whole series of brain-possessing animals, so far as Cuvier felt himself justified to go. And I avail myself of this concordance to define, agreeably with our common views, the aspects of the body in the adult Cephalopod, but in the terms which have been suggested by conclusions as to the essential conditions and wide extent of a possible predication of neural homologies.

The side of the body of a Cuttlefish or Squid denoted by the "neurœsophageal" ("subœsophageal" so called) brain-part, with the chief nervous extensions therefrom along the trunk, is the "neural aspect," its superficies the "neural surface" (fig. 9, N). The side of the body to which the "hæmœsophageal" (so-called "supraœsophageal") brain-part has been turned by the course of the gullet is the "hæmal aspect;" its superficies is the "hæmal surface" (ib. H). The "narrow space enclosed by the arms, which contains the mouth," together with the entire acetabular surface of those cephalic arms, is the anterior or "oral surface" (ib. A), answering to that so termed in all other Invertebrates, as is the homologous part in all Vertebrates. The opposite end of the body, with its appended fins, is the posterior or caudal end; what is usually called the upper surface in adult Cephalopods, as in all lower Mollusks and in Articulates, is the "hæmal one;" the opposite surface is the "neural" one. As here defined and illustrated, there can be at least no doubt as to the answerable aspects and surfaces in any Invertebrate possessing comparable centres and cords of the nervous system, with comparable centres, or hearts, of the vascular system. So the heart in man indicates the "hæmal" aspect (fig. 10, H), the myelon (*l*) the "neural" aspect (ib. N)

of his body, as in the animals below him whether vertebrate or invertebrate.

Fig. 11.



Profile diagram of head and brain of insect, with fore part of the neural and hæmal tracts or centres, in the position thereby indicated.

The letters of reference are :—*a*. Hæmœsophageal centre or "ganglion" =fore brain. *b*. Neurœsophageal centre or "ganglion"=hind brain. *c*. Œsophagus traversing the crura cerebri, or connecting-cords, *d*, to the neurostome in its course. *e*. Nerve (olfactory?) to antenna. *f*. Optic nerve. *g*. Ocellar nerve. *h*. Mandibular nerve. *i*. Lingual nerve. *k*. Maxillary and labial palpal nerves. *l*. Stomach, or alimentary axis. *m*. Heart, or hæmal axis. *n*. Ganglionic cords, or neural axis=myelon. *o*. Foremost thoracic centre or "ganglion."

Printed by Taylor and Francis, Red Lion Court, Fleet Street.